

1 **The effect of inter-group competition on intra-group affiliation in primates**

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17 Researchers from various disciplines have hypothesised that ecological conditions eliciting higher
18 levels of inter-group contest competition (IGCC) should favour the evolution of behavioural traits,
19 such as co-operation, altruism and friendship, which promote intra-group affiliation. Empirical
20 support for this hypothesis is, however, scarce and mainly available from humans. We tested if the
21 level of IGCC affects intra-group affiliation (i.e. intra-group grooming exchange) among male and
22 female non-human primates. To quantify intra-group affiliation, we used social network measures
23 and a grooming index. Our measure of IGCC combined frequency of inter-group encounters and
24 proportion of aggressive encounters ($N \text{ aggressive encounters} / \text{total encounters observed}$) and was
25 calculated separately for males and females. We ran our analyses on 27 wild groups of primates
26 belonging to 15 species (13 Cercopithecinae, 1 Colobinae and 1 Cebinae). Our results show that
27 females increased the density of their grooming networks and showed less variation in the number
28 of same-sex grooming partners in response to increased IGCC, whereas we found no significant
29 effect of IGCC on intra-group affiliation among males. Thus, our data provide partial support for an
30 effect of IGCC on intra-group affiliation, but suggest that the exact nature of such an effect is sex-
31 specific. These results may be explained by the differential costs and benefits males and females
32 experience during aggressive inter-group confrontations and by sex-specific differences in intra-
33 group affiliation.

34

35 **Keywords:** affiliation, collective action problem, competition, grooming, monkeys

36

37 **Highlights**

- 38 • We tested the hypothesis that inter-group competition affects intra-group affiliation
- 39 • We found the first partial support for this hypothesis in non-human primates
- 40 • Female primates increased intra-group affiliation when inter-group competition was high
- 41 • Intragroup affiliation in males was not affected by inter-group competition
- 42 • Inter-group competition may bear different cost/benefit for male and female primates

43

44 Inter-group contest competition (IGCC), where members of one group aggressively attempt to
45 access and monopolise valuable resources (e.g. food or water) at the expense of another group, is a
46 phenomenon observed in many group-living species (e.g. Rubenstein 1986; Kitchen and Beehner
47 2007; Radford 2008a; Crofoot and Wrangham 2010). The outcome of an aggressive inter-group
48 encounter can affect individual fitness (e.g. Radford and Fawcett, 2014), especially when ecological
49 conditions elicit frequent aggressive interactions between groups (e.g. due to habitat saturation or
50 food scarcity) that bear high cost/benefits payoffs (e.g. Mitani et al. 2010). Aggressive inter-group
51 encounters represent a typical example of collective action problems (Nunn and Lewis 2001;
52 Willems et al. 2013; Willems and van Schaik, 2015): groups where all members take part in the
53 aggressive confrontation are expected to have the best chances to win a fight (other things being
54 equal; e.g. group size, sex ratio) and thus gain access to the resources at stake. However, because
55 aggressive inter-group encounters also bear potential high costs for individuals (e.g. injuries or
56 death; Mitani et al. 2010), the risk of free-riding is high: some individuals could gain the benefits of
57 their group winning a fight with another group, without incurring any potential cost, by not taking
58 an active role in the aggressive confrontation (Nunn and Lewis 2001; Crofoot and Gilby 2012;
59 Willems et al. 2013; Willems and van Schaik, 2015).

60 Researchers have hypothesised that strong intra-group affiliation should reduce the
61 probability that animals in a group free-ride during collective action problems (Alexander and
62 Borgia 1978; Choi and Bowles 2007; Puurtinen and Mappes 2009). Thus, individuals from groups
63 where intra-group affiliation is strong should out-perform groups with weak intra-group affiliation
64 during inter-group confrontations, because everybody is taking part in the interaction. These groups
65 should then gain overall fitness benefits. Under this scenario, individuals in populations that face a
66 high level of IGCC should become progressively more affiliative towards their group members over
67 evolutionary time, thereby increasing the overall intra-group affiliation of the group. Furthermore,
68 individuals from groups where intra-group affiliation is strong should also be more likely to take
69 part in collective actions (such as protecting a food source from other groups) than individuals from

70 groups with weak intra-group affiliation (Conradt and List 2009; Miller et al. 2013). Following this
71 logic, researchers from a range of different disciplines, including evolutionary biology (Reeve and
72 Hölldobler 2007), behavioural ecology (Wrangham 1980; Sterck et al. 1997), psychology (West et
73 al. 2006; van Vugt and Park 2009) and anthropology (Haas 1990; Choi and Bowles 2007), have
74 predicted that a high level of IGCC should favour the evolution of behavioural traits which promote
75 intra-group affiliation, such as social bonding and parochialism (Alexander and Borgia 1978; Reeve
76 and Hölldobler 2007).

77 Several mathematical models, that support the hypothesis that the level of IGCC has a
78 positive effect on the evolution of intra-group affiliation, have been developed (e.g. Reeve and
79 Hölldobler 2007; Bowles 2009). However, empirical tests of this hypothesis are sparse and have
80 mostly focused on the proximate link between IGCC and intra-group affiliation. There is consistent
81 experimental evidence in humans showing that co-operation increases when groups are competing
82 with one another compared to situations without inter-group competition; this effect is independent
83 from kin relationships amongst group members (Erev et al. 1993; West et al. 2006; Tan and Bolle
84 2007; Puurtinen and Mappes 2009). This evidence has led some authors to propose that the
85 extensive period of warfare that our ancestors faced in the Pleistocene and Holocene has driven the
86 evolution of group-beneficial behaviours, such as in-/out-group categorisation in humans (Choi and
87 Bowles 2007; Bowles 2009).

88 For non-human species, data on the proximate effect of IGCC on intra-group affiliation are
89 relatively scarce (for a review: Grueter 2013), although the same principles should apply to all
90 taxonomic groups (see e.g. Wrangham 1980; Reeve and Hölldobler 2007). A few studies have
91 focused on post inter-group encounter allo-preening and allo-grooming, as a measure of intra-group
92 affiliation (Radford 2008a), as these two behaviours have important social functions in many
93 mammals and birds (e.g. they promote agonistic support and food tolerance; Dunbar 1991; Ventura
94 et al. 2006; Radford 2008a). In the co-operatively breeding green woodhoopoe (*Phoeniculus*
95 *purpureus*) the frequency and duration of allo-preening between group members increases

96 following a conflict with another group (Radford 2008a, b, 2011). Conversely, in captive tufted
97 capuchin monkeys (*Cebus apella*) visual interactions between groups did not result in increased
98 grooming exchange within the group (Polizzi di Sorrentino et al. 2012). Another measure of
99 affiliation that has been used is spatial proximity between group members. In chimpanzees (*Pan*
100 *trogodytes*) and spider monkeys (*Ateles geoffroyi*) individuals were found to stay closer together
101 when feeding in the home range of a neighbouring group (i.e. an area where the risk of a conflict
102 with another group is high) than when feeding in their home range (Aureli et al. 2006; Mitani et al.
103 2010). However, all of these studies have tested the immediate effects of inter-group encounters on
104 intra-group affiliation. It remains unclear if such effects are only short-lived and thus temporary
105 (e.g. an emotional response to the stress of the encounter; Radford 2008a, 2011; Polizzi di
106 Sorrentino 2012), if such an increase in affiliative behaviour occurs primarily between already
107 closely bonded partners and/or those who have actively participated to the inter-group encounter
108 (i.e. affiliation is partner specific), or if such behavioural responses to inter-group encounters would
109 indeed lead to an overall more general increase in intra-group affiliation.

110 To our knowledge, only two studies (Cheney 1992; Grueter 2013) have attempted to test the
111 generality of the hypothesised relationship between IGCC and intra-group affiliation across a
112 number of different species. Cheney (1992) used allo-grooming (hereafter grooming) distribution
113 (averaged across individuals of the same group) as a measure of group affiliation in non-human
114 primates. She predicted that animals would increase their effort to distribute their grooming more
115 evenly to their potential grooming partners, instead of mostly grooming with fewer individuals, the
116 higher the level of IGCC they faced. Grueter (2013) also investigated non-human primates and used
117 the average grooming time per species as a measure of intra-group affiliation. These two studies
118 hypothesised that the proximate effect of IGCC on intra-group affiliation would extend beyond the
119 first few minutes after an inter-group encounter. Groups facing higher IGCC would have overall
120 stronger intra-group affiliation than groups facing a lower level of IGCC, irrespective of the timing
121 and occurrence of each inter-group encounter (Wrangham 1980; Sterck et al. 1997). Contrary to

122 what was predicted, IGCC was not found to have a significant effect on either grooming
123 distribution among group members (Cheney 1992) or on total grooming time (Grueter 2013).
124 However, these two studies could not effectively tackle some important issues. Cheney's (1992)
125 study was restricted to female primates and did not control for the phylogenetic relationship
126 between species. Grueter (2013) used a proxy of IGCC (i.e. home range overlap) that could equally
127 measure inter-group scramble competition (Wrangham 1980; Sterck et al. 1997). These factors
128 could potentially explain the discrepancy between the human and the non-human primate data.

129 The mixed results available on this topic so far make it difficult to determine if IGCC
130 played a key role in the evolution of group-beneficial behaviours (Choi and Bowles 2007; Bowles
131 2009) in non-human animals. Our aim was to analyse the effect of IGCC on intra-group affiliation
132 across primate social groups, using a phylogenetically controlled analysis and a variety of different
133 measures of intra-group affiliation. We measured the level of IGCC by combining the frequency of
134 inter-group encounters and the proportion of aggressive encounters (independently calculated for
135 males and females). Intra-group affiliation, using grooming distribution, was measured by three
136 different variables: (a) the evenness of grooming, assessing the distribution of grooming effort
137 across potential grooming partners (following Cheney 1992), (b) the inter-individual variation in the
138 number of grooming partners, and (c) grooming network density. If IGCC elicits intra-group
139 affiliation in primates, we predicted that, in groups with high IGCC, animals would increase their
140 effort to distribute their grooming more evenly to their group companions, inter-individual variation
141 in grooming partner numbers would be low, and more individuals would be involved in grooming
142 interactions (high network density). Due to the scarcity of data available on a wide range of primate
143 taxa our dataset is mostly composed of Cercopithecinae (See supplementary table 1), i.e. of species
144 where grooming is the main affiliative behaviour and where females are the phylopatric sex.
145 Although not ideal, this allowed us to some extent to control for species-specific differences in
146 affiliative behaviours. In addition, we ran the analyses separately for male and female primates,
147 because intra-group same-sex affiliation can differ strongly between non-human primate species

148 (Wrangham 1980; Sterck et al. 1997; Crofoot and Wrangham 2010). Moreover, the two sexes differ
149 in their aggressive participation in inter-group encounters (Majolo et al. 2005; Kitchen and Beehner
150 2007; Crofoot and Wrangham 2010) and might have markedly different cost-benefit ratios of
151 IGCC. We did not consider grooming interactions between males and females, as a different set of
152 hypotheses (e.g. hired-gun hypothesis; Rubenstein 1986) than the ones tested here focus on hetero-
153 sexual grooming.

154

155 **METHODS**

156 *Data collection*

157 We used the ISI Web of Knowledge (© Thomson Reuters) to review the primatological literature
158 published between 1st January 1950 and 1st June 2011. We selected papers that contained detailed
159 data on grooming interactions between adult and sub-adult group members (e.g. a matrix of
160 grooming exchange) and on IGCC on one or more social groups. Data on juveniles and/or infants
161 were not included in the analyses. When these data were not available in a single paper, we
162 combined different published studies containing the relevant data collected on the same social
163 group within the same overall time period (see Supplementary material for further details).

164 Our literature review showed that published studies providing detailed data on grooming
165 and IGCC on a single social group are scarce. Therefore, we contacted colleagues working on
166 primates in the field, asking if they were willing to share with us the following data for each of their
167 study groups: study species, dates when data were collected, duration of the study (in months) and
168 location, group size (i.e. number of adults, sub-adults, juveniles and infants in the group), whether
169 the group was provisioned (i.e. the group relied extensively on human-provisioned food) or not, and
170 frequency of intra-group contest food competition (i.e. number of aggressive interactions over food
171 / hour). We also requested a matrix containing the proportion or frequency of grooming interactions
172 among the adult and sub-adult males and/or females of the study group. Finally, we requested the
173 following data on IGCC: frequency of inter-group encounters (i.e. number of inter-group encounters

174 / day) for the study group and proportion of inter-group encounters in which at least one adult male
175 and/or female from the study group was aggressive towards the other group (i.e. N aggressive
176 encounters for males/females divided by total encounters observed). We asked colleagues to give us
177 data for this latter variable separately for males and females. Moreover, we asked colleagues to
178 provide us with their definition of inter-group encounter (or we extracted this information from the
179 selected literature). The minimum distance between two groups, for an inter-group encounter to
180 occur, ranged between 15 and 100 meters across the studies included in our dataset, with an average
181 distance of approximately 50 metres. Aggression towards another group was defined as an animal
182 displaying threatening facial expressions or giving a threat call towards, chasing or biting one or
183 more animals from the other group.

184

185 *Data analysis*

186 The analyses presented here were based on 27 study groups from 15 species, 13 Cercopithecinae,
187 1 Colobinae and 1 Cebinae (males: 11 species, 19 study groups; females: 15 species, 25 study
188 groups; electronic supplementary table S1). We excluded from the analyses studies on 8 additional
189 species and 12 study groups because of missing data or because the study animals were not fully
190 habituated to researchers at time of data collection. The level of IGCC, our independent variable,
191 was quantified by multiplying the frequency of inter-group encounters (N of encounters/day) by the
192 proportion of these encounters that were aggressive. The level of IGCC had different values for
193 analyses done on males and females, as we calculated the proportion of aggressive encounters
194 separately for males and females (based on their involvement in them). We chose to combine these
195 two variables as each on its own does not accurately capture the level of IGCC. The frequency of
196 inter-group encounters does not imply anything about the nature of these encounters (i.e. aggressive
197 versus peaceful) while the proportion of aggressive encounters does not indicate anything about the
198 frequency in which these take place (e.g. 0.80 proportion of aggressive encounters twice a year or
199 twice per day would imply very different IGCC). Thus, by combining these two variables we

200 obtained a more informative measure of IGCC.

201 Matrices of grooming exchanges between group members were used to obtain three
202 measures of intra-group affiliation (our dependent variables). First, following Cheney (1992), we
203 used the Shannon-Wiener index (SWI; Wilson and Bossert 1971) to measure how an individual
204 distributes grooming to all the potential grooming partners (Supplementary material for further
205 details). The higher the value of SWI the more animals have evenly distributed grooming
206 relationships (i.e. they attempt to groom all of the available partners about equally). In addition to
207 the SWI, we calculated two commonly used social network metrics to quantify intra-group
208 affiliation (Borgatti et al. 2006; Wey et al. 2008). Because of the differences between studies in the
209 measures of grooming (e.g. percentage of grooming duration or simply frequency) we only
210 calculated network measures for binary networks (i.e. the presence/absence of a grooming
211 relationship) and not on bond strength. Our two network measures of intra-group affiliation were
212 standard deviation of the out degree and density (Borgatti et al. 2006). Standard deviation of the out
213 degree (SDOD) measures the inter-individual variation in the number of partners groomed. A low
214 SDOD value indicates that all group members groom a similar number of partners while a high
215 SDOD indicates that the number of grooming partners is skewed between group members. Density
216 measures the number of existing grooming relationships in relation to all possible grooming
217 relationships. All network metrics were calculated using UCInet 6 (Borgatti et al. 2006). The three
218 dependent variables were not significantly correlated to one another (Spearman pair-wise
219 correlations; all $P > 0.28$), suggesting that our indices of intra-group affiliation measured different
220 aspects of grooming distribution.

221 We controlled for four biologically relevant variables, which may affect the level of IGCC
222 and/or overall intra-group affiliation (electronic supplementary methods for further details): study
223 period length (measured in months), group size (number of animals in the social group, including
224 juveniles and infants), intra-group contest competition (aggressive events/hour) and provisioning
225 (binary variable: yes/no). We also controlled for additional variables that could bias our results,

226 including a ‘data quality’ variable (see electronic supplementary methods for details).

227

228 *Statistical analyses*

229 All the analyses were run considering data on each social group as a single data point, as IGCC and
230 intra-group affiliation are not likely to solely be species-specific traits and can vary significantly
231 across populations/groups (for a similar approach see Majolo et al. 2012). We ran phylogenetically
232 controlled generalized least square regression models (PGLS) in R 2.14.0 (R Development Core
233 Team 2011), using the CAPER 0.4 package (Orme et al. 2012). The phylogenetic tree for the
234 analyses was obtained from the 10ktree primate phylogeny version 2 (Arnold et al. 2010). We
235 derived lambda via maximum likelihood estimation as provided in CAPER.

236 All together we ran three models for each sex, with each of these models containing our
237 independent variable (level of IGCC) and the four additional control variables, namely study period
238 length, group size and intra-group contest competition as covariates, and provisioning (2 levels) as
239 confounding factor, which was dummy-coded. In addition, we ran the same analyses separately on
240 the two variables that we used to construct our measure of IGCC (i.e. the frequency of inter-group
241 encounters per day and the proportion of aggressive inter-group encounters for males/females). The
242 results for these models were representative of our overall results and are thus only presented in the
243 supplementary material (electronic supplementary tables S2-S5).

244

245 **RESULTS**

246 *Females*

247 A phylogenetic signal was detected for the standard deviation of the out degree (SDOD; Lambda =
248 0.97) and for density (Lambda = 0.76), but not for the Shannon-Wiener index (SWI; Table 1). The
249 level of IGCC was not significantly related to SWI (Table 1). Conversely, and supporting our
250 predictions, females showed significantly less variation in their number of grooming partners (i.e.
251 lower SDOD; Figure 1) and had significantly denser grooming networks (Figure 2) when levels of

IGCC were higher (Table 2). Among the control variables, we found that group size significantly affected SWI (larger groups had less evenly distributed grooming) and SDOD (larger groups had less variation in their number of grooming partners; Table 1). In addition, a higher level of intra-group contest competition resulted in generally denser grooming networks. The other control variables had no significant effect on intra-group affiliation (Table 2).

Males

A phylogenetic signal was detected in the model for SWI ($\lambda = 1$) whereas λ was equal to zero in the models on SDOD and density (Table 2). Contrary to our predictions, the level of IGCC had no significant effect on any of our affiliation measures (Table 2). For the control variables, we found that study period as well as group size affected SWI, i.e. grooming was more evenly distributed the longer the study period and the smaller the group size. Furthermore, group size also affected grooming network density: smaller groups had denser grooming networks than larger groups. The other control variables had no significant effect on grooming distribution.

DISCUSSION

In contrast to previous reports (Cheney, 1992; Grueter, 2013), our study is the first to provide partial support for the hypothesis that IGCC affects intra-group affiliation and suggests that the exact nature of this effect is sex specific. In males, the level of IGCC had no significant effect on grooming distribution. In females, the level of IGCC had a positive and significant effect on the variation in the number of grooming partners and on grooming network density, but not on SWI. Our findings on female primates, therefore, corroborate hypotheses from socio-ecological models (Alexander and Borgia 1978; Wrangham 1980; Sterck et al., 1997) and evolutionary biology (Reeve and Hölldobler 2007), and are in line with what has been found, and expected to occur in humans (Haas 1990; West et al. 2006; Choi and Bowles 2007; van Vugt and Park 2009). Because the data available for our analysis were mostly from Old World monkeys, we do not know if these finding

278 also extend to New World Monkeys. In addition, many species of New World monkeys are known
279 to show very little grooming (Dunbar 1991) and intra-group affiliation would have to be measured
280 differently in those species; however, we would expect to find a similar relationship between IGCC
281 and intra-group affiliation using appropriate affiliation measures.

282

283 *Sex differences*

284 By maintaining less varied and denser networks of intra-group affiliation, female primates may be
285 better able to cope with high levels of IGCC. Other things being equal (e.g. group size) females in
286 strongly affiliated groups might more effectively out-compete other groups and access/monopolise
287 resources (e.g. shelter or water) that are essential to maximise their reproductive outputs. The fact
288 that we only found an effect in females but not males is interesting. As males usually take a more
289 active role in aggressive inter-group encounters than females (Majolo et al. 2005; Kitchen and
290 Beehner 2007) and have been reported to have strong social bonds even in species with male
291 dispersal (Silk 1994; Mitani 2009; Schülke et al. 2010; Young et al 2014), a positive effect of IGCC
292 on intra-group affiliation was predicted to occur among males. The lack of support for this
293 prediction in males may be explained by two main factors. Firstly, the benefits and costs of
294 aggressively taking part in inter-group encounters differ between the two sexes. The benefits males
295 can gain from winning an encounter with another group are likely to be highly skewed in favour of
296 the dominant male, whereas in females benefits are expected to be more evenly distributed (Cheney
297 1992; Kitchen and Beehner 2007; Crofoot and Wrangham 2010). This might explain why overall
298 levels of same-sex affiliation are not affected by IGCC in males whereas female affiliation patterns
299 are affected. By out-competing another group, every female can potentially gain benefits like access
300 to food and reduced risk of immigration by infanticidal males, although these benefits could be
301 somewhat greater for dominant and/or lactating females (Sterck et al. 1997). Conversely, the main
302 benefits that males can gain during/following aggressive confrontations with other groups are
303 opportunities for extra-group copulations and/or for emigration, and defence of receptive females in

304 their group (Kitchen and Beehner 2007; Crofoot and Wrangham 2010). These benefits are likely to
305 not be shared equally by group males as, for example dominant males often monopolize mating
306 opportunities (e.g. Majolo et al. 2012). Indeed, it has been shown that aggressive participation in
307 inter-group encounters in males largely depends on the age and dominance status of the animals
308 (Majolo et al. 2005; Kitchen and Beehner 2007). Secondly, as all species in our sample are female
309 phylopatric, social relationships among dispersing males may be much more variable and
310 opportunistic than those in females, and be based on other behaviours (e.g. agonistic support) than
311 grooming (Schülke et al. 2012), which for lack of data could not be included into our analysis.
312 IGCC may affect male social relationships but this might not be reflected in the grooming network.
313 Thus, taken together, socio-ecological factors and the different cost/benefits of participation to inter-
314 group confrontations for the two sexes may modulate the effect that IGCC plays on intra-group
315 affiliation and more data are needed to further assess if and how IGCC affects affiliation among
316 males.

317

318 *Confounding variables*

319 The control variables showed that group size was a significant predictor of intra-group affiliation in
320 four of our six models, although the effects of group size on our dependent variables were small in
321 terms of the actual model coefficients. It is well known that group size affects the response of
322 animals to collective action problems as well as the outcome of inter-group encounters (Crofoot and
323 Gilby 2012; Willems and van Schaik, 2015). Group size also affects individual behaviour and has
324 been shown to have fitness consequences for individual animals (Majolo et al., 2008). Therefore,
325 group size is expected to modulate the relationship between IGCC and intra-group affiliation, which
326 is supported by our results. Since all of the species in our dataset are female phylopatric, the
327 relationship between grooming and IGCC may also be affected by kinship, that is, females in
328 species/populations facing a higher level of IGCC might have larger matriline, which in turn may
329 result in larger and denser grooming networks. In our dataset, we could not control for kin-

relationships (as kinship data were not available for most of the study groups in the dataset) but this would be an interesting hypothesis to test in future studies. By including group size into the models, however, we aimed to control for these effects in our analyses.

From non-human primate to humans

When comparing the effect of IGCC on intra-group affiliation in humans and non-human animals (Crofoot and Wrangham, 2010), three considerations have to be made. First, unlike many non-human primates, in human hunter-gatherer societies both sexes can disperse and establish long-distance and long-lasting social bonds and co-operative relationships (e.g. Apicella et al. 2012). As such, differences in social structure and inter-individual relatedness in humans societies compared to non-human primates could have an effect on how IGCC affects intra-group affiliation. Second, inter-group conflicts in non-human animals and human warfare may be two behaviourally different phenomena (Crofoot and Wrangham 2010). Human warfare in small scale societies, despite lacking the complex structure, strategic approach and forced recruitment of soldiers typical of military confrontations, is often characterized by social norms (e.g. participation in warfare as a sign of adulthood) and punishment rules (e.g. social isolation or reduced power) that favour individual contribution to aggressive encounters (Haas 1990). These factors should act on limiting the occurrence of free-riding and the risk posed by collective action problems in humans compared to non-human primates (Nunn and Lewis 2001; Crofoot and Gilby 2012; Willems et al. 2013; Willems and van Schaik, 2015). Similarly, the different risk posed by collective action problems can explain why the effect of IGCC on intra-group affiliation appears to be stronger in cooperative breeding birds (Radford 2008a, b, 2011) than in the primate species included in our study. In cooperatively breeding species, group members are often genetically related, share resources with one another (Radford and Fawcett, 2014), and groups are generally small; all conditions that reduce the risk of collective action problems (Willems and van Schaik, 2015). Conversely, our dataset was mostly composed of species living in large groups where the benefits and costs of intense IGCC are

356 likely to be skewed across group members. Third, inter-group conflicts in non-human animals and
357 human warfare may bear different consequences for individual fitness. Deaths resulting from inter-
358 group aggressive confrontations are thought to have been common during the course of human
359 evolution (Haas 1990; Choi and Bowles 2007; but see Fry and Söderberg 2013). Conversely, deaths
360 are relatively rare during inter-group encounters in non-human vertebrates and mostly observed in a
361 small number of species (e.g. lions and anthropoid primates: Packer et al. 1990; Mitani et al. 2010).
362 Therefore, there might have been stronger evolutionary pressure for an adaptive link between IGCC
363 and intra-group affiliation in the human lineage than in non-human primates or in other
364 phylogenetic taxa.

365 In conclusion, our study provides partial support for the hypothesis that IGCC affects intra-
366 group affiliation, similar to what has been shown in humans and in cooperatively breeding birds.
367 The fact that a link between IGCC and intra-group affiliation was found in females but not in males,
368 suggests different cost/benefit ratios of inter-group encounters for the sexes. The generality of our
369 findings to non-human primate species not included in this study, and to other taxa, is limited by the
370 scarcity and patchiness of data on this topic. When data become available, further studies will be
371 needed to test the effect of factors that we could not analyse here, such as social organization,
372 breeding system, relatedness and participation patterns in inter-group encounters. In addition, data
373 on more species are required and different measures, especially measures involving bond strength,
374 for intra-group affiliation should be explored. Despite the limitations of our study, our analyses
375 suggest for the first time that IGCC has the potential to affect intra-group affiliation in non-human
376 female primates.

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388

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494

495 Table 1: PGLS results on the effect of the level of IGCC and of the control variables on the three
496 measures of intra-group affiliation among females (n=25; significant results in bold).

Independent variables	Model No. - Dependent variables								
	Model #1 - SWI			Model #2 - SDOD			Model #3 - Density		
	Lambda = 0			Lambda = 0.97			Lambda = 0.76		
	Estimate \pm SE	t	P	Estimate \pm SE	t	P	Estimate \pm SE	t	P
Level of IGCC	0.12 \pm 0.36	0.34	0.74	-18.67\pm4.56	-4.10	<0.001	0.32\pm0.14	2.26	<0.03
Study period	0.14 \pm 0.08	1.75	0.10	-0.12 \pm 1.12	-0.11	0.92	0.06 \pm 0.04	1.58	0.12
Provisioning	-0.03 \pm 0.21	0.14	0.89	-4.27 \pm 2.96	-1.44	0.17	0.05 \pm 0.083	0.57	0.58
Group size	-0.01\pm0.00	-3.21	<0.01	-0.07\pm0.02	-2.91	<0.01	-0.00 \pm 0.09	0.03	0.97
Level of intra-group contest competition	-0.10 \pm 0.18	-0.56	0.58	-0.97 \pm 2.52	-0.39	0.70	0.07\pm0.00	-4.62	<0.001
Intercept	1.59\pm0.31	5.07	<0.001	16.99 \pm 12.06	1.41	0.18	0.60\pm0.24	2.51	0.02

497

498

499 Table 2: PGLS results on the effect of the level of IGCC and of the control variables on the three
500 measures of intra-group affiliation among males (n=19; significant results in bold). ^f denotes the
501 model for which the Lilliefors normality test was significant (indicating that the model residuals
502 were not normally distributed)

Independent variables	Model No. - Dependent variables								
	Model #1 ^f - SWI			Model #2 - SDOD			Model #3 - Density		
	Lambda = 1			Lambda = 0			Lambda = 0		
	Estimate ± SE	t	P	Estimate ± SE	t	P	Estimate ± SE	t	P
Level of IGCC	-1.95±2.76	-0.71	0.49	161.33±157.90	1.02	0.33	-0.05±0.20	-0.24	0.81
Study period	6.95±2.56	2.71	<0.02	-63.88±133.84	-0.48	0.64	-0.19±0.17	-1.10	0.29
Provisioning	1.54±0.84	1.82	0.09	77.57±102.0	0.75	0.46	-0.23±0.13	-1.71	0.11
Group size	-0.04±0.00	23.59	<0.001	-4.40±2.79	-1.58	0.14	-0.01±0.00	-2.26	<0.05
Level of intra-group contest competition	-0.49±0.64	0.76	0.46	-7.59±79.62	-0.09	0.93	0.22±0.10	2.08	0.06
Intercept	-6.04±8.17	0.74	0.47	317.85±219.48	1.45	0.17	0.81±0.28	2.83	<0.02

503

504 **Figure 1:** Scatter plots showing the relationship between the level of IGCC (ln-transformed), on the
505 y axis, and the standard deviation of out degree (SDOD) among female primates.

506

507 **Figure 2:** Scatter plots showing the relationship between the level of IGCC (ln-transformed) and
508 the density of grooming networks among female primates.